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Notes on the effect of mechanical pressure on the roots of Vicia Faba

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According to the second law of Hertwig,* "the axis of the mitotic figure typically lies in the longest axis of the protoplasmic mass, and division therefore tends to cut this axis at a right angle." Pflüger † and Driesch, ‡ experimenting with sea-urchin eggs, found that Hertwig's law held true even when the eggs had been compressed, and, as a result of the pressure, the long axis of the body was modified.

Conditions among plants do not always verify this law. Berthold § has shown that the cells of the cambium layer may divide lengthwise, in which case the mitotic figure would lie in the shortest axis of the body. Kny, || from his experiments of pressure on the division wall of plants, comes to the conclusion that the orientation of the mitotic figure, and with it the position of the division wall, may be influenced by pressure.

My work has been done with the purpose primarily of seeing if there is a definite effect of pressure on the mitotic figure, and secondarily of studying the morphological changes that take place in the compressed root-cells. The problem was given me by Professor H. M. Richards, whom I wish to thank for his helpful suggestions.

The material used in the work was *Vicia Faba*, whose roots are large and well adapted for experimental purposes. Roots of *Zea Mays* and *Helianthus annuus* were tried, but gave poor results.

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* Hertwig, O. Welchen Einfluss übt die Schwerkraft auf die Teilung der Zellen? Jenaische Zeitschrift **18**: —. 1884.

† Pflüger, E. Über die Einwirkung der Schwerkraft und anderer Bedingungen auf die Richtung der Zelltheilung. Arch. ges. Physiologie **34**: 607–616. 1884.

‡ Driesch, H. Entwicklungsmechanische Studien IV. Zeitschrift wiss. Zoologie **55**: —. 1893.

§ Berthold, G. Studien über Protoplasmamechanik. Leipzig, 1886.

|| Kny, L. Ueber den Einfluss von Zug und Druck auf die Richtung der Scheidewände in sich theilenden Pflanzenzellen. Ber. Deut. Bot. Gesell. **14**: 378–391. 1896.

The methods used in the experiments were of the simplest kind. The seeds were germinated and allowed to grow normally for three or four days (roots having secondary roots were never used). The roots were then placed between two plaster of Paris blocks in order to have the pressure lateral. The blocks were held together by different widths of elastic bands, the amount of pressure depending on the number and the width of the bands used. The roots remained under pressure usually during twenty-four hours, the actual time being from one P. M. to one P. M., in which case the roots were fixed during the secondary period ot maximum growth as determined by Kellicott.* Some roots were compressed during twelve hours only; in this case they were killed at eleven P. M. during the primary period of maximum growth. The roots were fixed in alcohol acetic, sublimate acetic, Flemming's fluid, and chromic acid. Alcohol acetic was found to be the best fixative. Serial sections, 5 μ in thickness were made, and stained with iron haematoxylin, which proved to be the most satisfactory stain. Control experiments were carried out under the same conditions, the roots being fixed at the same periods and the sections stained in the same manner.

Seventeen roots were compressed and sectioned. These may be divided into three groups:

1. Those least compressed, the pressure varying from 650 to 1000 grams. Exp. I, II, VIII, IX, XV;
2. Those with a medium amount of compression, the pressure varying from 1000 to 1400 grams. Exp. VII, XII, XIV;
3. Those with a maximum amount of compression, varying from 1400 to 2000 grams. Exp. III, IV, V, VI, X, XI, XIII, XVI, XVII.

The table of measurements shows the number of experiments performed, the time during which pressure was applied, the length and approximate thickness of the roots after compression, and finally the total amount of pressure. This amount of pressure was determined empirically only. The width of the crack between the blocks was measured before the roots were taken out, records being made of the number of strips of pasteboard necessary just to fill the crack. The blocks were kept with the bands upon them. To estimate the amount of pressure: the number of cardboard strips that had been determined before was placed between the blocks; the upper block was then fastened in a clamp on a standard and a weighing pan attached to the lower block; weights were then applied until the blocks were stretched apart enough to allow the cardboard strips to slip out.

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* Kellicott, W. E. The daily periodicity of cell division and the elongation of the root of *Allium*. Bull. Torrey Club **31**: 529–550. 1904.

TABLE OF MEASUREMENTS.

No. of experiment.	Time of compression.	Length of root after pressure.	Thickness of root after pressure	Total amount of pressure
I	24 hours.	14 mm.	.66 mm.	858 gm.
II	“	8 “	1.045 “	860 “
III	“	9 “	.38 “	1559 “
IV	“	12 “	.45 “	1650 “
V	“	12 “	.75 “	1902 “
VI	“	11 “	.74 “	1553 “
VII	“	13 “	.605 “	1103 “
VIII	“	7 “	.735 “	958 “
IX	“	6 “	1.020 “	958 “
X	“	5 “	1.035 “	1759 “
XI	“	7 “	.775 “	1759 “
XII	12 hours.	8 “	.828 “	1359 “
XIII	“	8 “	.750 “	2050 “
XIV	“	7 “	1.615 “	1253 “
XV	“	7 “	.805 “	662 “
XVI	10 hours.	10 “	.500 “	1625 “
XVII	“	10 “	1.025 “	1625 “

Very little of importance can be deduced from the thickness of the compressed roots since a measurement was not taken before the pressure was applied. As a result there are many cases giving seemingly contradicting results. For example, in experiment IX, after a pressure of *958* grams, the root measured 1.02 mm. in thickness; in experiment X, however, after a pressure of *1759* grams, the root measured 1.03 in thickness. This could probably be explained if the measurements of the roots before pressure were known. In the first seven experiments the roots used were of approximately equal size. Here the average thickness of roots affected by the minimum amount of pressure is .85 mm.; by the maximum amount of pressure, .58. In either case the normal root has been greatly compressed.

An examination of the material shows that contrary to the view of Kny and to the results of Pflüger and of Driesch, pressure has had no effect on the mitotic figure or division wall in the root cells of *Vicia Faba*. At first it was thought that the pressure had caused an increased number of transverse and oblique spindles. In one series a row of transverse spindles was found in the periblem layer at a point near the meristematic region. The control series, however, showed transverse spindles in an equally anterior region, and also as many oblique spindles as had been found in the compressed roots. In no way did the mitotic figure

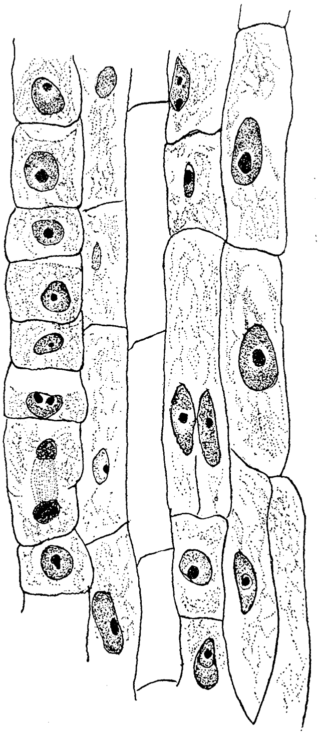

FIGURE 1. A median longitudinal section through a root to which 858 grams of pressure had been applied. Note the empty cells in which the split will take place, also the degenerating plerome cells on either side. The periblem layer is only slightly affected by the pressure. × 530.

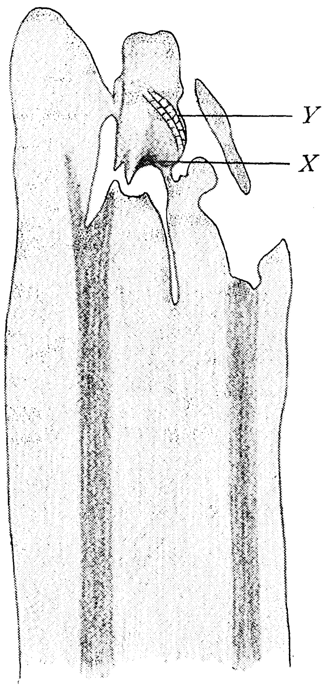

FIGURE 2. A low power sketch of the condition found in a root to which 1560 grams of pressure had been applied. The dark area represents the periblem tissue in which rifts have occurred. X = periblem cells which have been displaced. Y = plerome cells which also have been displaced.

seem to be affected by the pressure. In one case, I noticed a fragmentation of nucleoli taking place in almost every case, but as this was observed in one series only, it was thought to be due to some other cause than pressure.

A few interesting morphological points were noticed in the changes taking place in the cells of the compressed roots. In all cases, splits or rifts in some stage of formation were seen in the tissues. The beginnings of these splits can be found in the least compressed roots. The first indication of a definite split was the appearance of cells which had lost their entire contents, still retaining, however, their cell walls. These cells were found either in the extreme layer of plerome cells or just within the plerome layer. On either side of this layer were plerome cells in different stages of degeneration. In general, the protoplasm had become vacuolated and had shrunken from the wall. In some cases their nuclei showed signs of abnormality (see FIGURE 1).

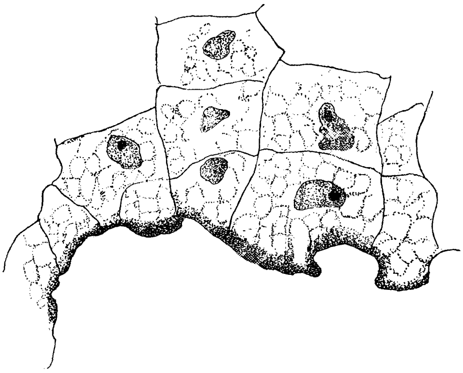

FIGURE 3. Displaced periblem cells from region *X* in FIGURE 2. The cells show the vacuolization of the protoplasm and also the general tendency of the cells to assume their normal condition. × 530.

In the second group of experiments, which includes the roots that were subjected to a pressure varying from 1000 to 1400 grams, the plerome cells were still more vacuolated, and definite splits had appeared not only in the extreme layer of plerome cells but also throughout the central portion. Even with this pressure but few changes were observed in the periblem and dermatogen tissues.

In the third group of experiments, which includes the roots subjected to an extreme amount of pressure varying from 1400 to 2000 grams, marked changes had taken place. The plerome cells were well broken up. Splits had appeared in the periblem layer, and groups of both plerome and periblem cells were greatly displaced (see FIGURE 2).

In general, the greatest amount of injury was found in the region directly posterior to the initial meristematic region. Roots which had been subjected to the greatest amount of pressure showed cavities and rifts in all regions and in many cases displacement of single cells or masses of cells. The protoplasm of the cells on the edges of the rifts was very much vacuolated and the nuclei were distorted in many cases; a few, however, had assumed a normal condition (see FIGURE 3). Plerome cells, which had been forced into the extreme anterior portion of the root, showed evidences of further differentiation into the future vascular system (see FIGURE 4). Thus we may conclude that not even a maximum amount of pressure, nor an absolute change in environment will entirely stop or affect the normal development of the cells of *Vicia Faba*.

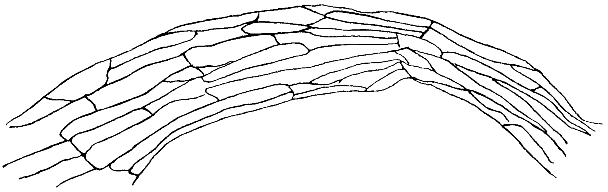

FIGURE 4. Displaced plerome cells from region *Y* in FIGURE 2, showing elongated cells which have become further differentiated into fibrovascular tissue. × 530.

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